
STUDIES IN NEOTROPICAL
PALEOBOTANY. VI.
THE LOWER MIOCENE
COMMUNITIES OF PANAMA—
THE CUCARACHA
FORMATION¹

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ABSTRACT

The Cucaracha microfossil flora is the third in a series of four lower Miocene assemblages studied from southern Central America (Uscari—Costa Rica; Culebra, Cucaracha, La Boca—Panama). Nineteen palynomorphs have been identified (Selaginella, monolet fern spores types 1–3, Cyathea, Ceratopteris, Pteris, cf. Antrophyum, trilete fern spores types 1–2, Cryosophila and Manicaria-type palm pollen, Ilex, Compositae, Alchornea, Alfaroa/Engelhardia, Crudia, Eugenia/Myrcia, and Rhizophora). The paleocommunities include a fern marsh, with associated palms, fringed seaward by mangroves, and bordered on the surrounding uplands by versions of the tropical wet, tropical moist, and premontane forests. Evidence for higher-altitude vegetation and communities of drier to arid aspect (open forests, savannahs) continues to be meager for Tertiary floras in the region. Affinities of the flora are distinctly Central and North American, consistent with other paleontological and biogeographic data, as well as paleophysiographic reconstructions for southern Central America. Paleoclimatic conditions were similar to those presently prevailing in coastal, lowland, and mid-altitude (1,200–1,500 m) habitats. Frequent and extensive volcanic activity documented for the region likely disrupted the vegetation, resulting in a shifting mosaic of short-term, more open communities. This may account for a paleobotanical record reflecting primarily dense forests on the slopes, while the few fossil mammalian faunas contain remains of browsers and grazers, suggesting more open forests and savannahs.

The Cucaracha Formation is lower Miocene in age and outcrops along both sides of the Panama Canal between Hodges Hill and the Pedro Miguel Locks (Stewart & Stewart, 1980). It belongs to a complex of three Tertiary formations similar in age and lithology known to contain plant microfossils. The lowermost is the Culebra, and study of these palynomorphs has been completed (Graham, 1988). The Cucaracha Formation lies directly on the Culebra in local areas, and thus stratigraphic relationships are relatively clear, even though the region is considerably faulted. The position of the La Boca Formation is more difficult to determine because nowhere does it lie directly on the Cucaracha. However, the Pedro Miguel does overlie the Cucaracha, and in other areas it interfingers with the La Boca. Thus the three formations are presently

considered sequential in age, with the Cucaracha being intermediate between the slightly older Culebra and slightly younger La Boca formations. For more detailed discussion of the geology of the pollen-bearing strata see Graham et al. (1985).

The Cucaracha Formation consists mainly of bentonitic clay shales, tuffaceous siltstones, and sandstones with lenses of conglomerates, carbonaceous shales, and lignite. A well was drilled through the formation in 1958 (Hole No. PA-33, latitude 9°01'N, longitude 79°38'W, Cucaracha Reach Widening Studies, Panama Canal Commission), and the log shows the above sequence repeated many times through the 40.8-m section. Near the base is a conglomerate containing abundant oyster shells. The sequence is typical of a tectonically active, coastal, estuarine environment, and the lignites

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TABLE 1. Identification and numerical representation of fossil palynomorphs from the lower Miocene Cucaracha Formation, Panama. Figures are percentages based on counts of 100. Samples 57–59 are from the lower lignite in the section, and samples 62–66 are from the upper lignite. Samples 57 and 66 contained abundant fungal spores, and preservation of pollen and other spores was fair to poor.

| | Sample Number | | | | | | |
|----------------------------|---------------|----|----|----|----|----|----|
| | 57 | 58 | 59 | 62 | 63 | 65 | 66 |
| Selaginellaceae | | | | | | | |
| <i>Selaginella</i> | — | — | — | — | — | — | 5 |
| Monolete fern spore | | | | | | | |
| Type 1 | 16 | 6 | 62 | 7 | 14 | 1 | 3 |
| Type 2 | 3 | — | — | — | 1 | 1 | 7 |
| Type 3 | 6 | 65 | 16 | 72 | 77 | 77 | 38 |
| Cyatheaceae | | | | | | | |
| <i>Cyathea</i> | — | — | — | — | — | — | 3 |
| Pteridaceae | | | | | | | |
| <i>Ceratopteris</i> | — | — | 1 | — | — | — | — |
| <i>Pteris</i> | — | — | 1 | — | — | — | — |
| Vittariaceae | | | | | | | |
| cf. <i>Antrophyum</i> | — | 3 | 3 | — | — | — | — |
| Trilete fern spore | | | | | | | |
| Type 1 | — | — | — | — | — | — | 4 |
| Type 2 | — | — | — | — | — | — | 3 |
| Palmae | | | | | | | |
| <i>Cryosophila</i> -type | — | — | — | — | — | — | 2 |
| <i>Manicaria</i> -type | 11 | 13 | 8 | 6 | 6 | 4 | 13 |
| Aquifoliaceae | | | | | | | |
| <i>Ilex</i> | — | — | — | — | — | — | 1 |
| Compositae | — | — | — | 2 | — | — | — |
| Euphorbiaceae | | | | | | | |
| <i>Alchornea</i> | — | — | 1 | 1 | — | 1 | — |
| Juglandaceae | | | | | | | |
| <i>Alfaroa/Engelhardia</i> | — | — | — | 1 | — | — | — |
| Leguminosae | | | | | | | |
| Caesalpinioideae | | | | | | | |
| <i>Crudia</i> | — | — | — | — | — | — | 2 |
| Myrtaceae | | | | | | | |
| <i>Eugenia/Myrcia</i> | — | — | — | — | — | — | 2 |
| Rhizophoraceae | | | | | | | |
| <i>Rhizophora</i> | 60 | 13 | 7 | 9 | — | 11 | 17 |
| Unknowns | | | | | | | |
| Type 1 | 3 | — | — | — | — | — | — |
| Type 2 | 1 | — | 1 | 2 | 2 | 5 | — |

indicate warm-temperate to tropical conditions. Extensive vulcanism is indicated by the tuffs (water-lain volcanic ash) and the basalt that caps the section.

THE COLLECTING LOCALITY

Samples were obtained from a roadside exposure along road K-2, about 0.8 km northwest of the intersection with K-15 in the Gaillard Cut section of the Canal. At this site there is a small utility building, and about 4 m above and to the left is a conspicuous conglomerate layer about 1 m thick (see figs. 7, 8 in Graham et al., 1985). This layer terminates abruptly and continues on the other side of the building about four meters lower in the section. This is one of the many minor faults in the region and is a convenient marker for the locality. Ten samples were collected (our locality C, samples 57a–66) and seven contained plant microfossils. Three of these (57–59) came from a 0.6-m layer of lignitic shale about six meters below the conglomerate and to the right (facing the slope) of the utility building. Four (62, 63, 65, 66) came from a similar lignitic shale about four meters above the conglomerate; all samples were spaced horizontally about two meters apart. About 0.7 km further to the right (NW) is the site from which Whitmore & Stewart (1965) reported a mammalian fauna from the Cucaracha Formation, all with distinct North American affinities.

MATERIALS AND METHODS

Extraction and processing techniques are described in Graham (1985). Slides are labeled Pan C, Cucaracha, sample, and slide number (e.g., Pan C, Cucaracha, 66, 1). Location of specimens on the slides is by England Slide Finder coordinates (e.g., ESF R-34, 3–4). All materials are deposited in the palynology collections at Kent State University.

SYSTEMATICS

Nineteen palynomorphs have been identified from the Cucaracha assemblage (Table 1), and two others were recovered whose biological affinities could not be established (unknowns types 1 and 2). Illustrations, descriptions, and other data are provided for each pollen/spore type, but since all have been recovered from other Gulf/Caribbean Tertiary formations, the information is synoptic, and references are provided to more detailed discussions. These formations, with references, are as follows: Gatuncillo (middle(?) to late Eocene, Pan-

ama; Graham, 1985), San Sebastian (middle to late Oligocene, Puerto Rico; Graham & Jarzen, 1969), Uscari (early Miocene, Costa Rica; Graham, 1987a), Culebra (early Miocene, Panama; Graham, 1988), and Paraje Solo (late Miocene, southeastern Veracruz, Mexico; Graham, 1976). A map of the geographic distribution and a chart summarizing the age of the formations are given in Graham (1987b; for other aspects of the identification procedures see Graham 1985: 507–508). Present ranges of the modern analogs within the Neotropics and ecological data are summarized after each description, with more detailed summaries provided in the paleobotanical publications previously cited. These data are based on field observations, personal communication with specialists in the various plant groups, and the literature, especially Croat (1978), D'Arcy (1987), Hartshorn (1983), Tryon & Tryon (1982), and Woodson & Schery (1943–1980). Terminology for vegetation types follows Holdridge (1947; Holdridge et al., 1971), used by Croat (1978) and Hartshorn (1983) for describing the plant communities of Panama and Costa Rica.

SELAGINELLACEAE

Selaginella (Figs. 1, 2). Spherical, amb circular to oval-triangular; trilete, laesurae frequently obscured by dense sculpture and appearing mono-lete, straight, narrow, ca. 20–24 μm long, extending nearly to spore margin; echinate, echinae short (ca. 2–3 μm), occasionally curved, dense, bases broad; wall ca. 2 μm thick (excluding echinae); 26–30 μm .

Other occurrences. Gatuncillo, San Sebastian, Uscari, Culebra, Paraje Solo formations.

Distribution. Widespread; usually moist, shaded habitats; typically low to mid altitudes but widespread altitudinally.

MONOLETE FERN SPORES

These spore types are produced by many members of the Blechnaceae and Polypodiaceae and cannot be referred to any one modern genus, especially in the absence of the ornamented exospore or perine. They are often assigned to the artificial genera *Laevigatosporites* (smooth forms) or *Verrucatosporites* (verrucate forms), and these range from Paleozoic to Recent. They occur in all of our Gulf/Caribbean Tertiary deposits studied to date, and multiple biological species are likely represented by each of the spore types described below.

Type 1 (Figs. 3, 4). Reniform; mono-lete, lae-

surae straight, narrow, 24–28 μm long, extending ca. $\frac{3}{4}$ spore length, inner margin entire; laevigate; 40–50 \times 30–40 μm .

This is one of the most abundant spores in the Cucaracha Formation, although percentages vary widely among the samples (Table 1). Figure 4 is a low-magnification view of part of a single field (negative-size portion) typical of samples where the spore is dominant. Ten specimens are evident in this field, and a thousand or more may occur on a slide.

Type 2 (Figs. 5, 6). This spore differs from Type 1 in having a slightly thicker wall and, therefore, is more consistently reniform in shape. The specimens range in size from 35 \times 20 μm (Fig. 5) to 42 \times 32 μm (Fig. 6).

Type 3 (Figs. 7–11). Reniform; mono-lete, laesura straight, narrow, 30–45 μm long, extending $\frac{3}{4}$ spore length, inner margin entire; verrucate, verrucae moderately low, conspicuous and dense, grading into less dense, widely spaced verrucae, shape irregular, ca. 3 \times 6 μm ; wall 2–3 μm thick; 35–55 \times 25–35 μm .

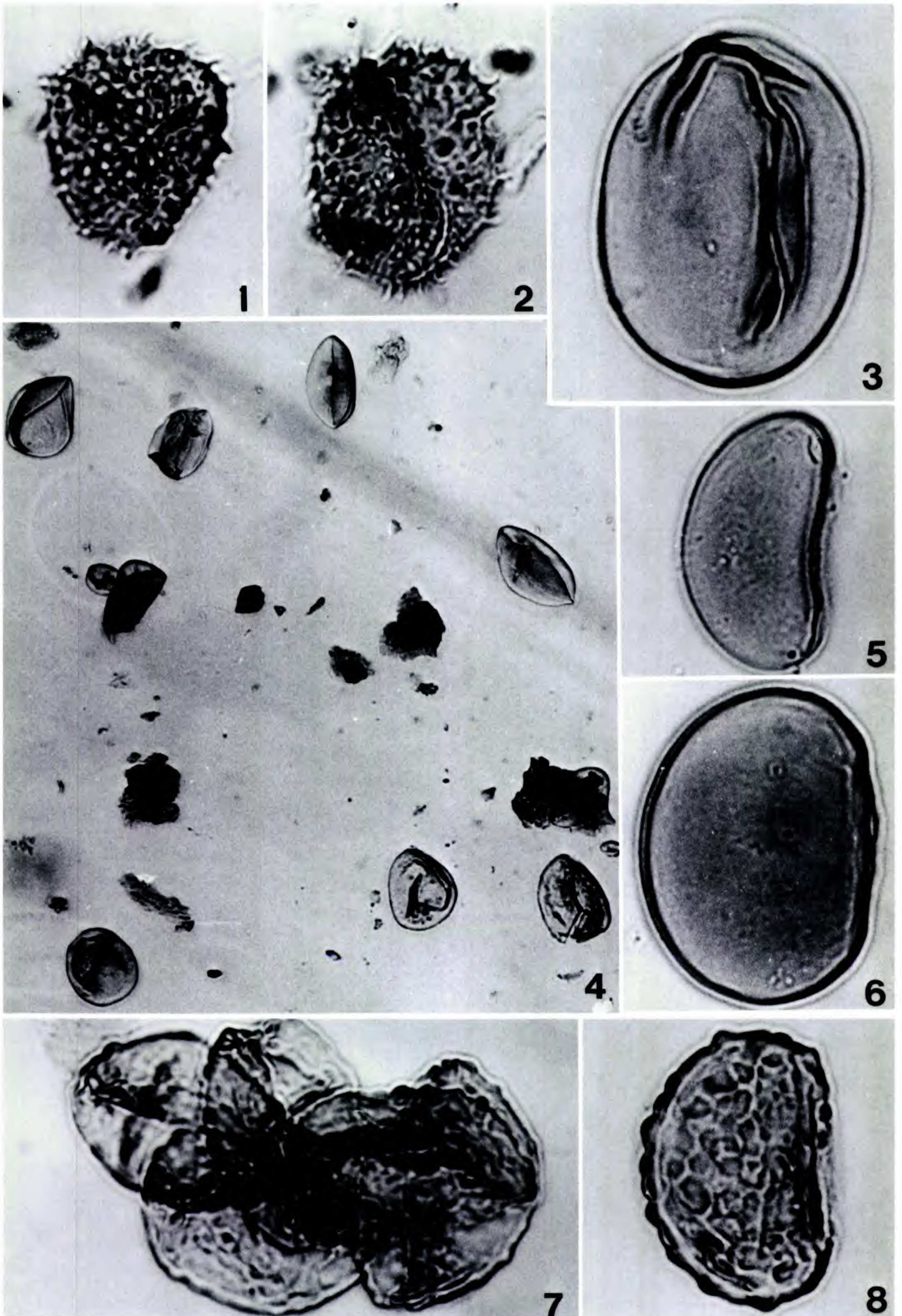
This is another spore that is dominant in several samples, almost to the exclusion of other microfossils (Table 1). In addition to individual specimens, many clusters of 5–20 loosely aggregated spores were evident on the slides (Fig. 7). This indicates that the Cucaracha sediments at this locality were accumulating directly under or immediately adjacent to a fern marsh, with little transport of the specimens.

The spores vary in size and density of the verrucae. Figure 8 illustrates a small specimen (ca. 37 μm), and Figure 9 a larger one (ca. 54 μm), while comparison of Figure 8 with Figure 11 shows the variation in the number of verrucae. Similar spore variation occurs within species as well as among species and genera of modern Blechnaceae and Polypodiaceae. As noted previously, more than one biological species, or genus, is likely represented by this spore type.

TRILETE FERN SPORES

Cyatheaceae

Cyathea. Amb oval-triangular, apices rounded; trilete, laesurae straight, narrow, 14–16 μm long, extending to spore margin, inner margin entire, bordered by lip 2–3 μm wide with punctae 1 μm diam.; distal surface finely punctate, proximal surface more laevigate near laesurae; wall 1.5–2 μm thick; 30–35 μm .



A few poorly oriented specimens of *Cyathea* were recovered from sample 66, but the genus is frequent in other Caribbean Tertiary deposits. According to Gastony & Tryon (1976) and Tryon & Tryon (1982: 207), the micropunctate forms represent *Cyathea*, while similar but smooth (laevigate) types are referred to the closely related *Alsophila*.

Other occurrences. San Sebastian, Culebra, Paraje Solo formations.

Distribution. Widespread, primarily montane forests and cloud forests; in Central America low rain forests usually at 1,500–2,000 m, but as low as 500 m.

Pteridaceae

Ceratopteris (Figs. 14, 15). Amb oval-triangular, spore margin undulating due to projecting sculpture elements; trilete, laesurae straight, narrow, 28–32 μm long, extending to spore margin, inner margin entire; wall coarsely and conspicuously striate, striae psilate, 3–4 μm wide, prominently developed on distal surface, less distinct approaching laesurae; wall 2–3 μm thick; 75–90 μm .

Other occurrences. Gatuncillo, Paraje Solo formations.

Distribution. Widespread, southeastern U.S. (Texas to Florida), southern Mexico, Central America, Antilles, South America; frequently aquatic, ditches, lagoons, river/lake margins, brackish waters; sea level to ca. 300 m.

Pteris (Fig. 13). Amb triangular, apices rounded; trilete, laesurae straight, narrow, 15–18 μm long, extending to spore margin, inner margin entire; distal surface with coarse, irregular verrucae, proximal surface more laevigate, flange ca. 6 μm wide, hyaline; wall 2 μm thick; 42–48 μm .

Other occurrences. Gatuncillo, San Sebastian, Uscari, Culebra, Paraje Solo formations.

Distribution. Mexico, Central America, the Antilles, and South America; openings or along margins of wet or cloud forests; sea level to ca. 2,000 m.

Vittariaceae

Cf. *Antrophyum* (Fig. 12). Amb triangular, apices rounded; trilete, laesurae relatively small in relation to spore diameter, straight, narrow, 12–15 μm long, extending ca. $\frac{2}{3}$ distance to spore margin, inner margin entire; laevigate; wall ca. 1.5 μm thick; 47–54 μm .

Other occurrences. San Sebastian (not figured in Graham & Jarzen, 1969), Culebra, and Paraje Solo formations.

Distribution. Hidalgo, Mexico, Central America, and the Antilles, to northern Argentina and southeastern Brazil; rain and cloud forests; elevations usually 100–1,500 m.

OTHER TRILETE FERN SPORES

Type 1 (Fig. 16). Amb oval-triangular; trilete, laesurae straight, narrow, 14–16 μm long, extending to or nearly to spore margin, inner margin entire; finely reticulate, reticulum becoming more irregular near laesurae; wall ca. 1.5 μm thick; 27–30 μm .

Other occurrences. Possibly Culebra Formation (larger specimen).

Type 2 (Figs. 17, 18). Amb oval-triangular; trilete, laesurae straight, narrow, 15–17 μm long, extending to or nearly to spore margin, inner margin entire; punctate, punctae circular (ca. 1 μm) to elongated (2–3 μm), slitlike and sinuous; wall 2 μm thick; 33–36 μm .

Other occurrences. Possibly Culebra Formation (larger specimen with more conspicuous slitlike punctae).

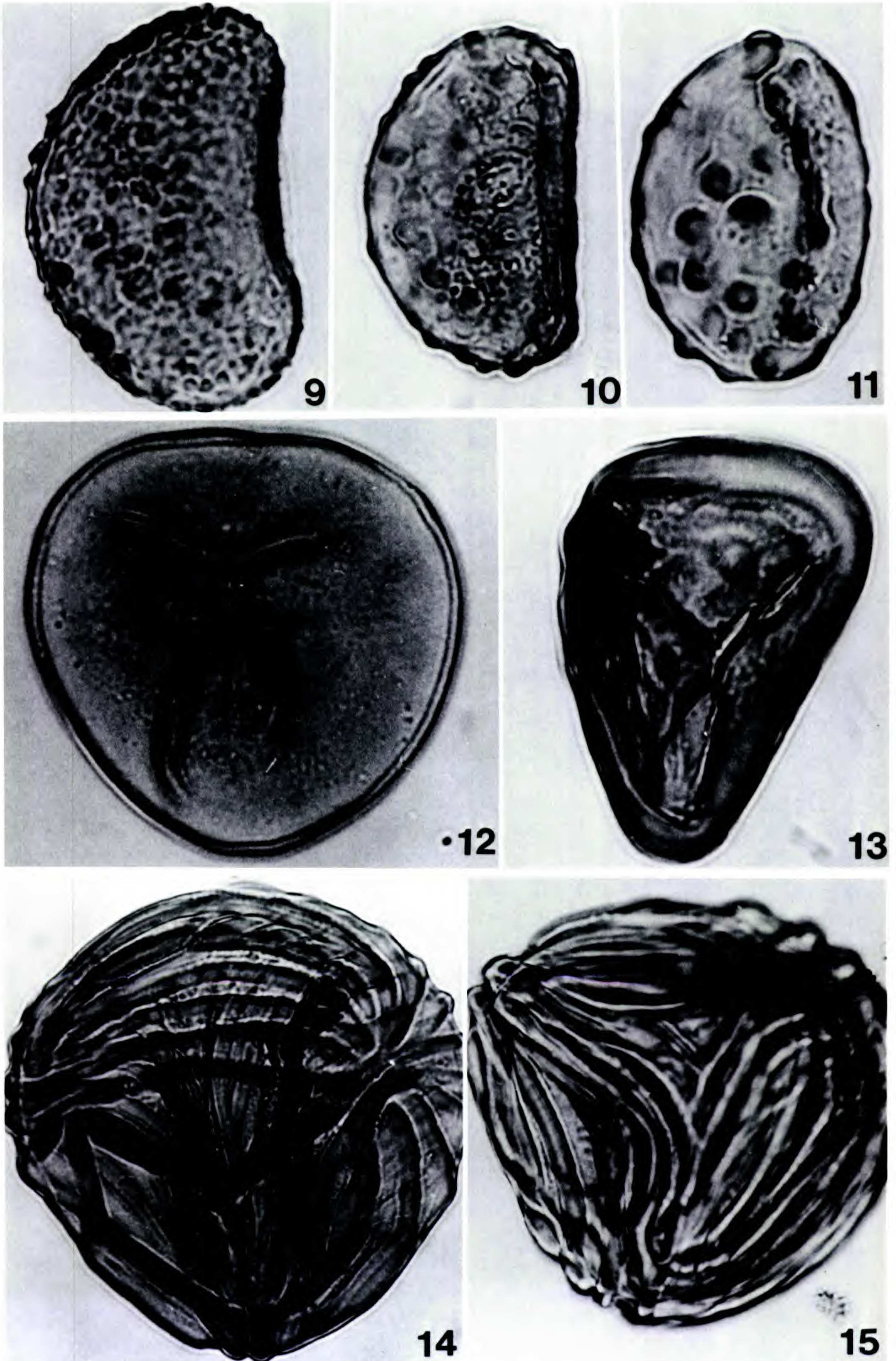
PALMAE

Cryosophila-type (Fig. 19). Prolate, amb oval; monocolpate, colpus straight, 22–24 μm long, extending entire length of grain, margin entire; tectate-perforate, wall 2 μm thick; reticulate, muri relatively broad (ca. 1–1.5 μm), flat, lumen ca. 2 μm in diameter on distal side, smaller approaching colpus; 31–33 \times 18–20 μm .

Other occurrences. Culebra Formation.

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FIGURES 1–8. Fossil spores from the Cucaracha Formation, Panama.—1. Selaginella (trilete scar evident). Pan C-66, 1, ESF R-34, 3–4.—2. Selaginella (trilete scar obscure, appearing monolete). Pan C-66, 1, ESF T-31, 3, 4. Monolete fern spore type 1.—3. Pan C-57, 1, ESF C-24, 4.—4. Overview (10 \times) in upper left corner of Pan C-59, 2 showing 10 monolete fern spore type 1 in single frame (partial field of view).—5. Monolete fern spore type 2 (small). Pan C-63, 1, ESF K-21, 2–4.—6. Monolete fern spore type 2 (large). Pan C-57, 1, ESF G-21, 2–4.—7. Loose cluster of monolete fern spore type 3. Pan C-62, 1, ESF G-33, 2.—8. Monolete fern spore type 3. Pan C-57, 1, ESF G-22, 1–3.



FIGURES 9-15. Fossil spores from the Cucaracha Formation, Panama.—9-11. *Monolete fern spore type 3*. Pan C-65, 1, ESF P-22, 3-4; Pan C-63, 1, ESF K-11, 2; Pan C-63, 1, ESF H-16, 1-2.—12. Cf. *Antrophyum*.

Distribution. Belize to Panama; tropical wet, tropical moist, premontane wet forests; low altitudes.

Manicaria-type (Figs. 20–22). Prolate; monocolpate, colpus straight, 30–36 μm long, extending nearly entire length of grain, inner margin entire; scabrate (to possibly microreticulate); trilete, wall 1.5 μm thick; 36–45 \times 20–24 μm .

Other occurrences. Gatuncillo, Culebra formations.

Distribution. Antilles, Central and South America; wet places; low altitudes.

Another palm pollen of the *Manicaria*-type was recovered but differs in size (25 vs. 36–45 μm ; Figs. 23, 24).

AQUIFOLIACEAE

Ilex (Fig. 25). Oblate-spheroidal, amb circular; tricolporoidate, colpi straight, 18 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin diffuse, pores obscure, situated at midpoint of colpus; intectate; clavate, wall ca. 3 μm thick (length of clavae); 27 \times 22 μm .

Other occurrences. Gatuncillo, San Sebastian, Uscari, Culebra, Paraje Solo formations.

Distribution. Widespread; mesic to slightly drier habitats; low to mid altitudes; Costa Rica—tropical and premontane wet lowlands, montane rain forest.

COMPOSITAE

(Figs. 26–28). Spherical, amb circular; tricolporate, colpi straight, short (ca. 10 μm), equatorially arranged, meridionally elongated, equidistant, pore oval, ca. 4 \times 2 μm , situated at midpoint of colpus; tectate, wall 2–3 μm thick; echinate, echinae short (ca. 2–3 μm), base broad, moderately dense (distance between spines ca. 3–4 μm); 23–27 μm .

Other occurrences. Uscari (rare), Culebra (rare), and Paraje Solo (relatively common) formations.

EUPHORBIACEAE

Alchornea (Fig. 29). Oblate, amb circular; tricolpate, colpi straight, 8–10 μm long (pole to equator), equatorially arranged, meridionally elongated, equidistant, extending within 6–7 μm of pole, inner

margin entire, distinct operculum; tectate, wall 2 μm thick; psilate to faintly scabrate; 15–21 μm .

Other occurrences. San Sebastian, Uscari, Culebra, Paraje Solo formations.

Distribution. Widespread; Panama—tropical moist, premontane wet, premontane rain forests; Costa Rica—alluvial soil in tropical wet lowlands, mid-altitude wet and rain forests, altitude range 300–2,000 m.

JUGLANDACEAE

Alfaroa/Engelhardia (Fig. 30). Oblate, amb oval-triangular; triporate, pores circular, ca. 2 μm , inner margin entire, equatorially arranged, equidistant; tectate, wall 1.5 μm thick; psilate; 21 μm .

Other occurrences. Gatuncillo, San Sebastian, Paraje Solo formations.

Distribution. Mexico, Central America; typically associated with lower to mid-altitude temperate forests.

LEGUMINOSAE

Caesalpinioideae

Crudia (Fig. 31). Prolate; tricolporoidate, colpi narrow, straight, 25 μm long, extending nearly entire length of grain, equatorially arranged, meridionally elongated, equidistant, pore area faint, circular, situated at midpoint of colpus; tectate but with occasional separation between sculpture elements, wall 1.5 μm thick; distinctly and coarsely striate, striae generally oriented parallel to long axis of grain, surface psilate, margins entire, occasionally appearing beaded from underlying pores in foot layer/endexine; 32 \times 20 μm .

Other occurrences. Gatuncillo Formation.

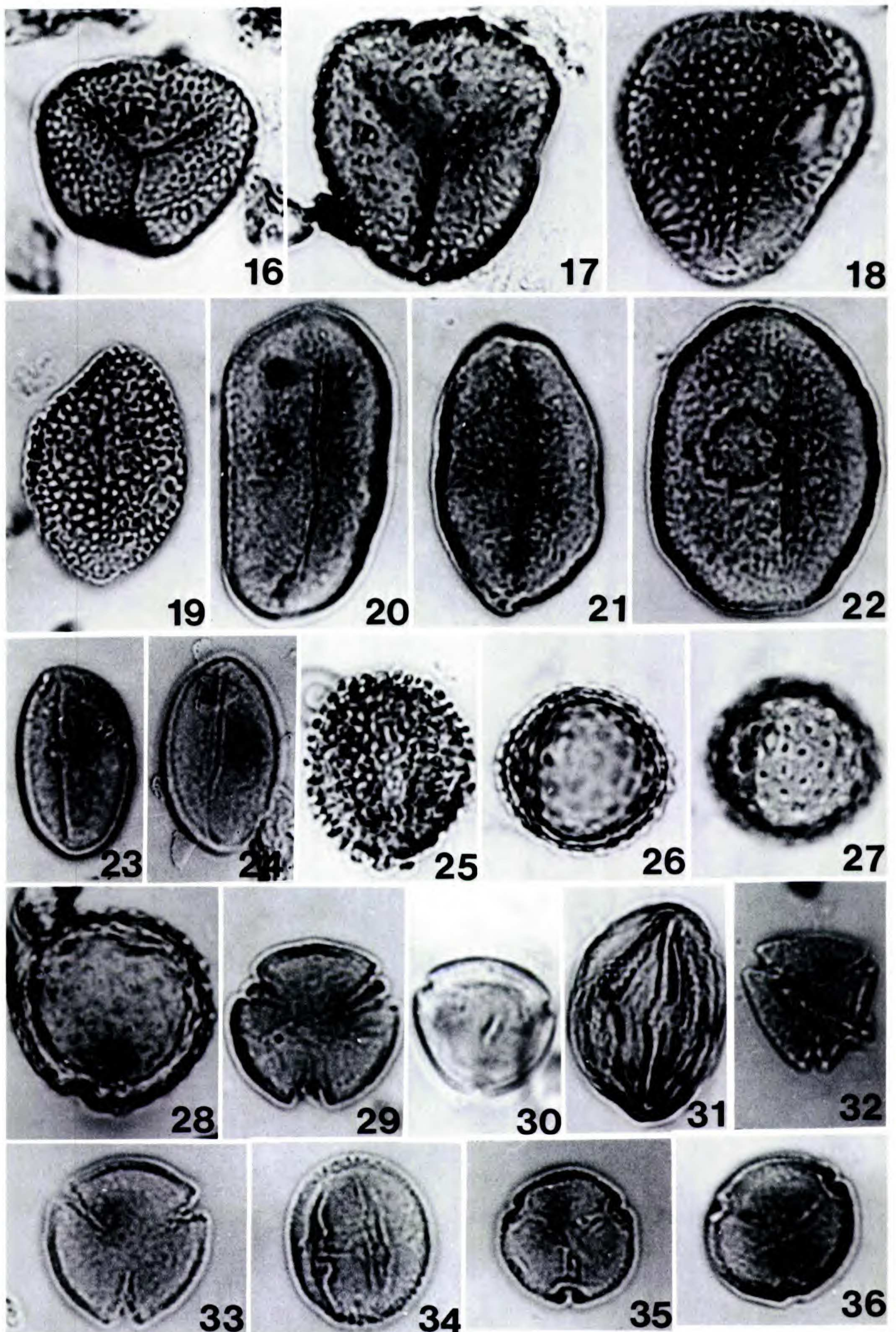
Distribution. Mainly Amazonian, often riverine; low altitude.

MYRTACEAE

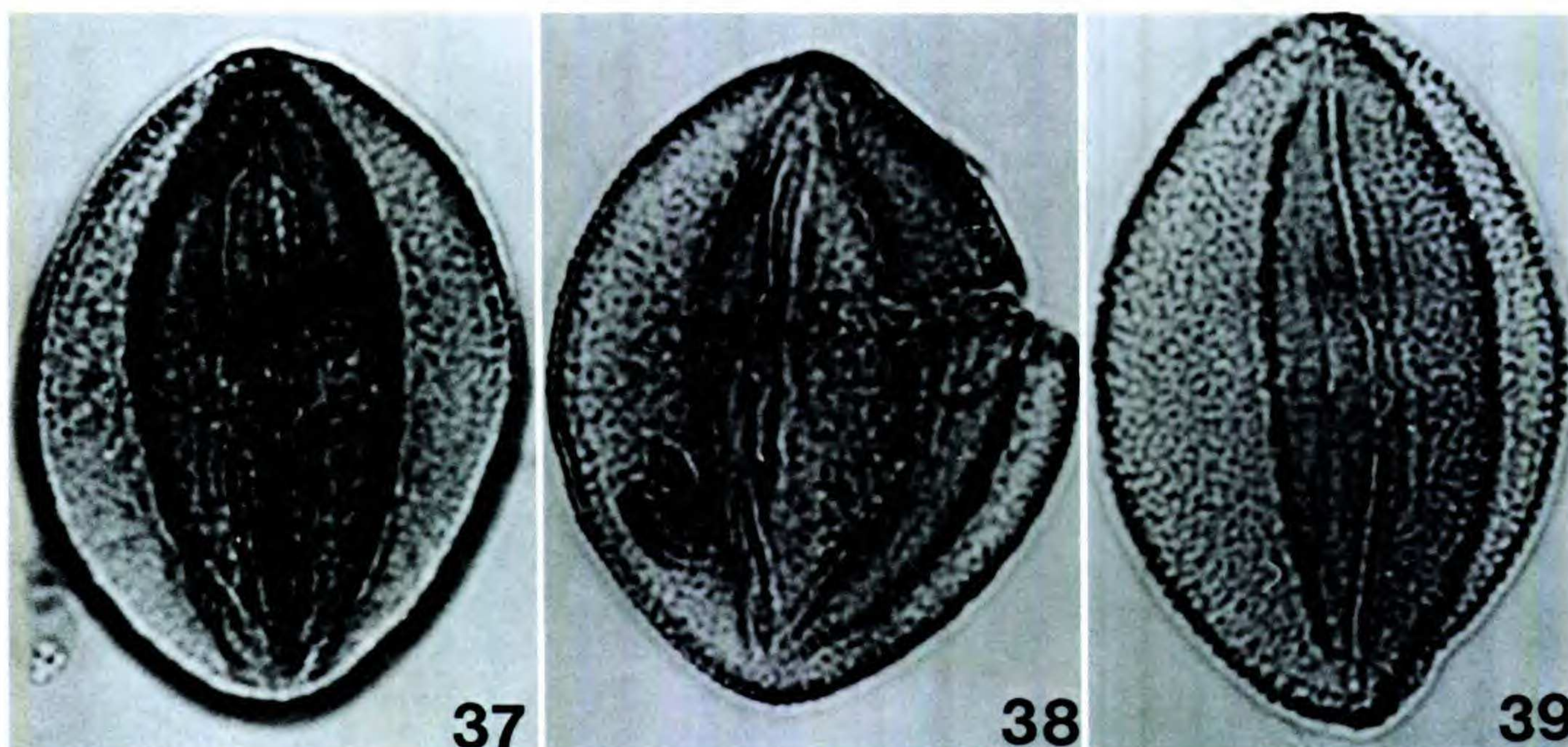
Eugenia/Myrcia (Fig. 32). Oblate to peroblate, amb triangular; tricolporate, colpi narrow, straight, 9 μm long, equatorially arranged, meridionally elongated, equidistant, syncolpate, pore ca. 1 μm diam., situated on equator at midpoint of colpus; tectate, wall thin (ca. 1.5 μm); faintly scabrate; 18 μm .

Other occurrences. Gatuncillo, San Sebastian, Uscari, Culebra, Paraje Solo formations.

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FIGURES 16-36. Fossil spores and pollen from the Cucaracha Formation, Panama.—16. Trilete fern spore type 1. Pan C-66, 1, ESF K-35, 1.—17, 18. Trilete fern spore type 2. Pan C-66, 1, ESF G-53, 3; Pan C-66, 1, ESF X-31, 1-3.—19. Cryosophila-type palm pollen. Pan C-66, 1, ESF P-33, 3.—20-22. Manicaria-type palm



FIGURES 37-39. Fossil pollen from the Cucaracha Formation, Panama. Unknown type 2. Pan C-59, 2, ESF Q-41, 1; Pan C-59, 2, ESF V-48, 3-4; Pan C-57, 1, ESF M-19, 1-3.

RHIZOPHORACEAE

Rhizophora (Figs. 33, 34). Prolate to prolate-spheroidal; tricolporate, colpi narrow, straight, 14-16 μm , apices acute, equatorially arranged, meridionally elongated, equidistant, costae colpi ca. 3 μm , pores elongated equatorially (colpi transversalis), 1 \times 4 μm , constricted at midpoint of colpus, inner margin entire; tectate-perforate, wall 2-3 μm thick; finely reticulate; 18-25 \times 16-20 μm .

Other occurrences. Gatuncillo, San Sebastian, Uscari, Culebra, and Paraje Solo formations.

Distribution. Widespread, southeastern U.S. to South America; warm-temperate to tropical habitats, coastal brackish waters; sea level.

UNKNOWN

Type 1 (Figs. 35, 36). Oblate, amb circular; tricolporate, colpi narrow, straight, 6-8 μm long, equatorially arranged, meridionally elongated, equidistant, syncolpate, pores circular to slightly elongated equatorially, costae pori, situated on equator at midpoint of colpus; tectate-perforate, wall ca. 2 μm thick; finely reticulate; 16-20 μm .

Type 2 (Figs. 37-39). Prolate; tricolporate,

colpi straight, 40-48 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire, costae colpi 5-7 μm wide, pore slightly oval, 3 \times 5 μm , situated at midpoint of colpus; tectate-perforate, wall 2 μm thick; finely reticulate; 43-55 \times 30-42 μm .

Other occurrences. Gatuncillo, Culebra, and Paraje Solo formations.

NUMERICAL REPRESENTATIONS

A total of 700 palynomorphs were tabulated from the Cucaracha material (100 from each of the seven samples; Table 1). Normally 200 pollen grains and spores are counted, but in the Cucaracha assemblage each sample was dominated by a single type, with all other forms collectively constituting only a small percentage of the flora. The most abundant microfossils were monolete fern spore type 3, monolete fern spore type 1, *Rhizophora*, and *Manicaria*-type palm pollen. Vascular cryptogams (ferns and *Selaginella*) totaled 71% of the flora, *Rhizophora* 17%, palms 9%, and all other angiosperm pollen 3%. Clearly, the sediments accumulated in a fern marsh with palms surrounding

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pollen (large). Pan C-59, 2, ESF N-43, 1-3; Pan C-59, 2, ESF K-28, 1-3; Pan C-59, 2, H-33, 4.—23, 24. *Manicaria*-type palm pollen (small). Pan C-59, 2, ESF N-25; Pan C-57, 1, ESF U-11, 3.—25. *Ilex*. Pan C-66, 1, ESF E-34, 3-4.—26-28. *Compositae*, Pan C-62, 1, ESF R-40, 3-4; Pan C-62, 1, ESF F-48, 2-4.—29. *Alchornea*. Pan C-59, 2, ESF H-21.—30. *Alfaroa*/*Engelhardia*. Pan C-62, 1, ESF F-48, 2-4.—31. *Crudia*. Pan C-66, 1, ESF H-40, 3-4.—32. *Eugenia*/*Myrcia*. Pan C-66, 1, ESF S-31, 2-4.—33, 34. *Rhizophora*. Pan C-57, 1, ESF C-27, 1; Pan C-57, 1, ESF D-18, 3.—35, 36. Unknown type 1. Pan C-57, 1, ESF F-19, 4; Pan C-59, 2, ESF S-41, 1-3.

and possibly intermingling with the ferns and with mangrove (*Rhizophora*) growing along the seaward margin of the depositional basin. It was a simple ecosystem in terms of community types, with little pollen of other associations being blown or washed into the basin from the surrounding landscape.

Another quantitative feature of the Cucaracha flora is the rapid change in this coastal vegetation over very short periods of time. Samples 57, 58, and 59 were from a lower lignite bed about 0.6 m thick. All samples were taken from about the middle of the seam and horizontally were about two meters apart. Yet sample 57 contained about 60% *Rhizophora* pollen, sample 58 had 65% type 3 monolet fern spores (with only 13% *Rhizophora*), and sample 59 had 62% type 1 monolet fern spore (with only 7% *Rhizophora* and 16% type 3 fern spore). The vertical difference between the samples was, at maximum, only a few centimeters, and in a rapidly accumulating, estuarine sedimentary basin this likely represents only a few to several hundred years. Within this brief time span, three different taxa dominated the site. The upper lignite layer was more uniform in composition, with monolet fern spore type 3 dominant in all samples (Table 1). Among the seven samples from the two lignite layers, *Rhizophora* ranged from absent (sample 63) to 60% (sample 57); monolet fern spore type 1 from 62% (sample 59) to 1% (sample 65); and monolet fern spore type 3 from 77% (samples 63, 65) to 6% (sample 57). There were apparently some habitat differences within and between the lignite layers, as well as differences in ecological preference between the ferns, because the percentages of monolet fern spore types 1 and 3 were reciprocal. These fluctuations evident in the pollen and spore assemblage are typical of estuarine habitats in tectonically unstable regions. Slight elevation of the land surface (or lowering of sea level) drains the lowlands marginal to the coast of salt water, and ferns dominate the freshwater habitats provided by inflowing rivers. With land subsidence marshes are inundated, the waters rendered brackish, and mangroves dominate the site. This sequence is repeated many times through the Culebra Formation, as evidenced by the alternating layers of lignites and lignitic shales; mud-, silt-, and sandstones; water-lain volcanic ash (tuffs); and the basal oyster-rich conglomerate.

PALEOCOMMUNITIES AND PALEOENVIRONMENTS

A limited number of paleocommunities are revealed by the Cucaracha flora. A fern marsh, with

associated palms and the floating fern *Ceratopteris*, are well represented. This freshwater assemblage was fringed seaward by mangroves (*Rhizophora*). Some indication of the inland vegetation is provided by a few spores of the tree ferns *Cyathea* and *Pteris*, and small amounts of pollen of *Alchornea*, *Alfaroa/Engelhardia*, Compositae, *Crudia*, *Eugenia/Myrcia*, and *Ilex*. These suggest tropical wet, tropical moist, and premontane forests on the adjacent slopes. It is likely that higher-altitude vegetation was meager, and its absence to poor representation in the microfossil record not just the result of exclusion from the sedimentary process. In other palynofloras (e.g., the San Sebastian flora of Puerto Rico and the Paraje Solo flora of Mexico), representatives from mid- to higher-altitude communities are common. Their poor representation in the Cucaracha flora is probably an accurate reflection of the kinds of communities occupying the low, insular landscape in the region at the time.

Pollen grains of the Gramineae, other species associated with savannah habitats, and dry to arid vegetation were not recovered, consistent with results from other Tertiary floras in Central America.

The paleoenvironment can only be characterized generally as tropical and probably similar to that presently prevailing at lower altitudes in the region (see Graham, 1985: 531–532). All palynomorphs recovered from the Cucaracha Formation occur in the modern vegetation of Panama.

TERTIARY FLORAS, FAUNAS, AND VOLCANISM IN SOUTHERN CENTRAL AMERICA

As data accumulate on the Tertiary floras of northern Latin America, it is becoming evident that little *paleobotanical* evidence is emerging for extensive savannah or open-forest habitats. The limited data do not preclude, however, more local, shifting, temporal stands of these communities in the Central American landscape. Such accommodation is necessary because of a seemingly anomalous situation developing between the kind of vegetation reflected in the Tertiary floras of Central America and the kind of habitats required by the few mammalian faunas known from the area. The palynofloras suggest that tall, dense tropical forests were prevalent on adjacent upland slopes, while the vertebrate faunas contain significant numbers of browsers (low open forests) and grazers (savannahs).

Tertiary palynofloras from Central America (see chart in Graham, 1987b) contain little or no grass pollen, or pollen of trees or shrubs characteristically associated with open forests or savannahs. An exception may be the few grains of *Acacia* pollen

found in the Paraje Solo and Culebra floras. Bartlett & Barghoorn (1973) found little evidence for savannah or drier open forests in Quaternary sediments from Gatun Lake, Panama, but Leyden (1984) reported the presence of more arid vegetation from Pleistocene deposits in Guatemala. The latter report, and the very small amounts of grass and *Acacia* pollen in Tertiary sediments, indicate that the list of Cenozoic paleocommunities for the region is still being developed. Nonetheless, the principal communities in the Cucaracha flora were likely the tropical moist, tropical wet, and pre-montane forests, with mangroves and fern and palm marshes occupying coastal and swamp habitats.

In contrast, browsers and grazers are the prominent components in the two principal Tertiary vertebrate faunas reported from Central America. Olson & McGrew (1941) described a fauna from the Pliocene Gracias Formation, in the Mejocote Valley of Honduras. In addition to *Amphicyon*, *Procamelus* (camel), and *Blickotherium* (mastodon), the most common remains were of the horses *Pliohippus* and *Neohipparion*. Whitmore & Stewart (1965) described a fauna from the Cucaracha Formation, ca. 0.7 km from the plant microfossil locality. In addition to the marsh- and swamp-inhabiting turtle and alligator remains, they reported five browsing ungulates: Equidae (*Anchitherium*, *Archaeohippus*), Rhinocerotidae (*Diceratherium*), Merycoidodontidae (*Merycochoerus*), and Protoceratidae (a selenodont artiodactyl).

The situation wherein fossil floras suggest forest while faunas, including the near-contemporaneous and adjacent Cucaracha fauna, reflect open forest and savannah on the uplands, is similar to that in the Tertiary biota of the western United States. A tentative explanation suggested for that region may apply to southern Central America. In a study of the Miocene Trout Creek flora of southeastern Oregon (Graham, 1963, 1965), representative megafossil species were not uniformly distributed through the 17-m section. In the middle part of the section there were numerous layers of sand and volcanic ash. Toward the top and bottom, the number and thickness of the ash layers decreased (Fig. 40). Megafossils were abundant in the upper and lower portions and were much less common in the middle part, where volcanic activity was greatest. Clearly the plant communities were disrupted by ejection of quantities of volcanic ash, the deforestation allowing sands to wash into the depositional basin from the surrounding landscape. Taggart et al. (1982; Taggart, pers. comm., 1987) suggested that the browsing and grazing faunas that characterize the middle and late Tertiary of western North America were exploitive, flourishing

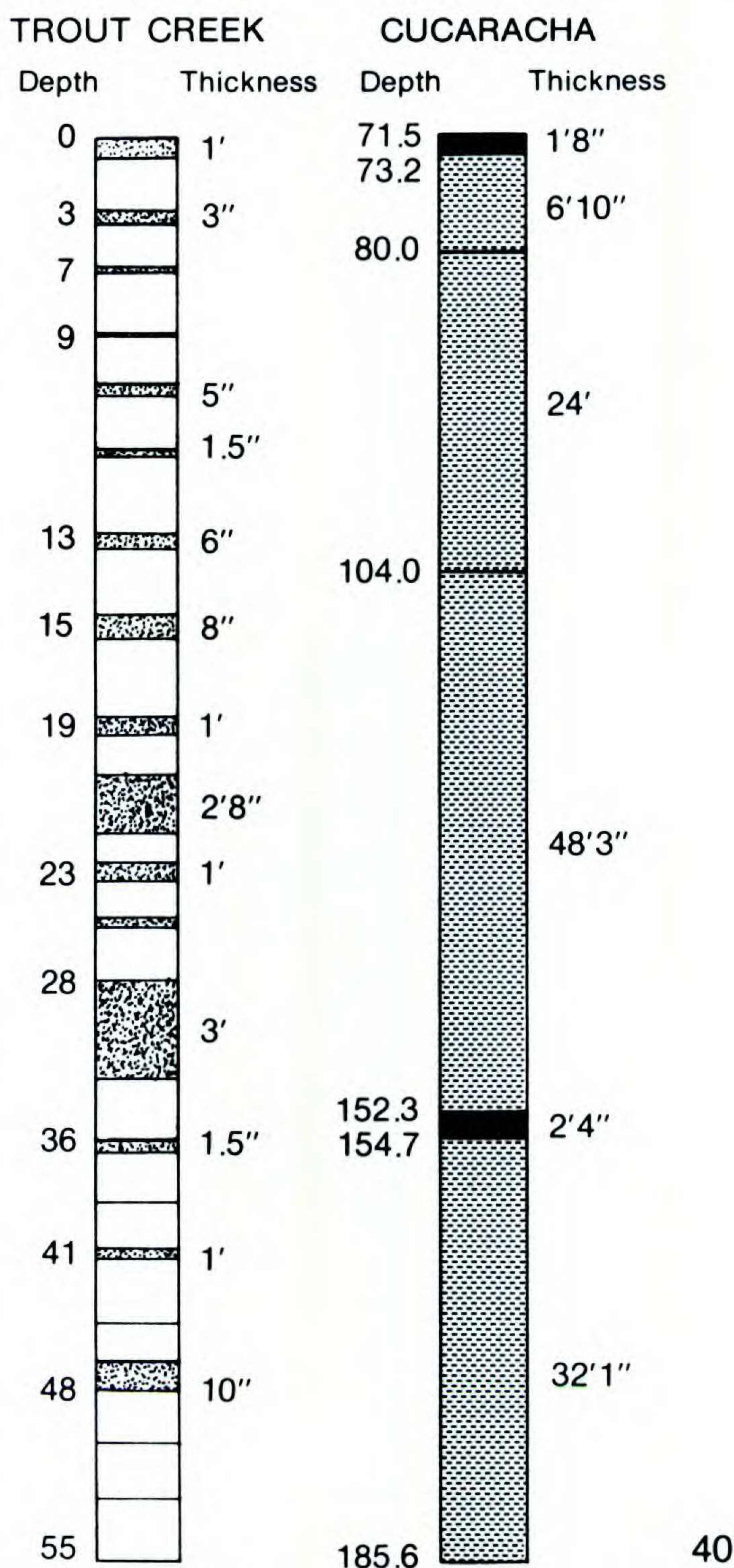
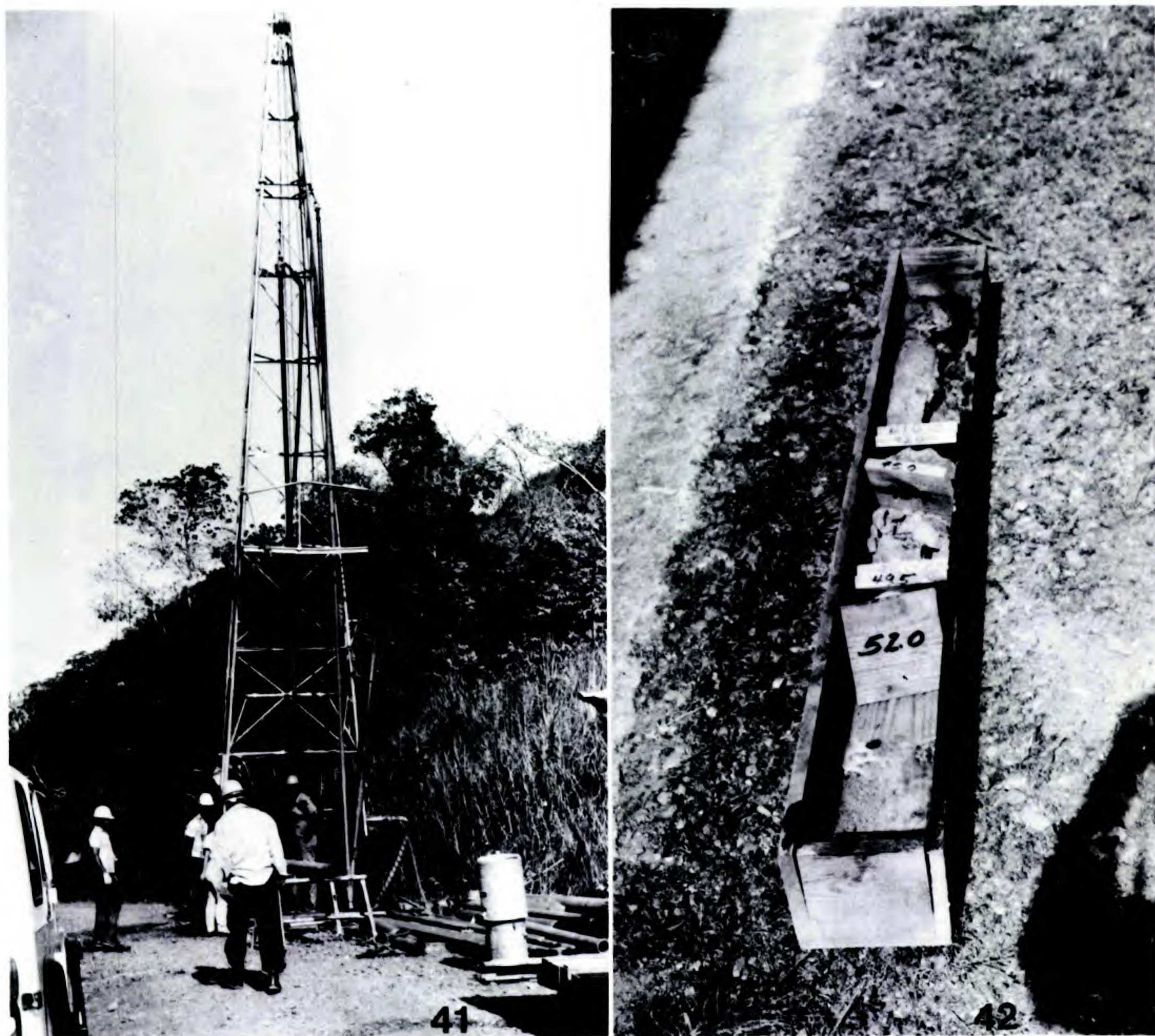


FIGURE 40. Stratigraphic sections from the Trout Creek (late Miocene, Oregon) and Culebra (early Miocene, Panama) formations. White = diatomite; stippled = sandstone and sandy volcanic ash; black = lignite, lignitic shale, or highly carbonaceous clay-siltstone; dashed = tuffs (water-lain volcanic ash) or clay-siltstones derived from erosion of tuffs. In both sections the plant megafossils (Trout Creek) and microfossils (Culebra) are associated with sediments indicative of frequent and extensive volcanic activity.

during recovery periods when open habitats were more extensive. The reduced vegetation, unfavorable preservation conditions in the accumulating sandy ash layers, and the relatively brief time spans involved minimized the representation of this recovery vegetation in the plant fossil record. During intervening times when volcanic activity was less,



FIGURES 41, 42. *Drilling operations and resulting core from the Cucaracha Formation, Canal region, Panama.*—41. Portable drill from truck bed.—42. Core from the Cucaracha Formation. Logs from these cores provide the descriptive lithologies (e.g., Fig. 40) used to characterize the general depositional environments of the microfossil assemblages. Photographs taken January 1986.

forests became more extensive and contributed the abundant plant remains preserved in the diatomite. Another factor is the resistant nature of the faunal remains favoring preservation, transport, and accumulation in the depositional basin.

Figures 41 and 42 illustrate the coring device and the cores derived from the Cucaracha and other Tertiary formations in the Canal region of Panama. A description of the lithologies along these cores is kept by the Panama Canal Commission in the form of drill logs. A portion of one log from the Cucaracha Formation is presented by Graham et al. (1985: 495, table 3) and is summarized in Figure 40. It is clear that volcanic tuffs (water-lain volcanic ash) are common throughout the section (e.g., at levels 154.7', 104.0', 80', and 73.2'), and the same is true for other Tertiary formations

in Panama. Basalt also caps many of the sections. If the pattern of Tertiary faunas with significant numbers of browsing and grazing elements, and Tertiary floras reflecting forested vegetation, persists in future studies, a shifting mosaic of brief, open, recovery vegetation in this volcanically active region may afford a reasonable explanation for the apparent differences in habitats suggested by the floral and faunal evidence.

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